Acta Œcologica, 1990, **11** (2), 191-213.

Development, growth and species richness on Brittany heathlands after fire

F. Forgeard

Université de Rennes-I,
Laboratoire d'écologie végétale,
Complexe scientifique de Beaulieu,
35042 *Rennes Cedex, France*

ABSTRACT

Vegetation development on Brittany heathlands after fire was studied. Two models were relevant to this. The fluctuating model was descriptive of events after low-intensity burning, where subsequent stump regeneration is largely responsible for regrowth. The re-colonization model was applicable to heathland after intense fire when stumps and soil seed banks were destroyed. Here three alternative routes could be followed; from initial bryophyte domination to mesophylic heath, to tall heath, or to pre-woodland birch scrub respectively. In general vegetation structure and heath composition after burning rapidly returned to that which existed before. Fire risk, as judged by accumulated biomass, was appreciable five to seven years after light burns, and ten to fifteen years after intense burns. In tall heath critical fire-risk threshold was equated with a biomass of about 50 t/ha and continuous horizontal structure.

KEY WORDS: Brittany, fire, heathland, vegetation dynamics, biomass, permanent line transects, AVL classification.

RÉSUMÉ

L'évolution de la végétation est suivie dans des landes bretonnes soumises à des incendies. Deux modèles de recolonisation ont été reconnus : le modèle de fluctuation (à partir de rejets de souches) après des incendies légers, et le modèle de succession secondaire après des incendies intenses. Dans ce cas, trois voies évolutives sont possibles. Elles vont des groupements bryophytiques à des groupements de landes mésophiles, de landes hautes ou des groupements préforestiers à bouleau. Les landes originelles se reconstituent généralement assez vite et identiques à ce qu'elles étaient avant le passage du feu. Les risques d'incendie sont à nouveau sérieux, 5 à 7 ans après un incendie léger, 10 à 15 ans après un incendie intense. Dans les landes hautes, le seuil critique de risque d'incendie correspond à une lande présentant une biomasse voisine de 50 t/ha et ayant une structure horizontale continue.

INTRODUCTION

Major changes have occurred in land use patterns of Brittany heathlands since the economic crisis of 1929-1934. Gradual abandonment of these low-production areas has often allowed vegetation to reach a pre-woodland stage. Re-afforestation in Brittany involving *Pinus sylvestris* and *Pinus maritima* has also progressed

Acta Œcologica 1146-609 X/90/02/191/23/$ 4.30/ © Gauthier-Villars

since the mid-nineteenth century, and these naturally re-seeding species have been particularly successful in invading mesophilic heathland. A recent study (FORGEARD, 1986) has shown that abandonment and re-afforestation together have increased heathland fire-risk. An average of 1,200 ha of Brittany heathland burns annually, and in the exceptionally dry year of 1976, the total was 7,800 ha.

Heathland fire parameters (soil-surface temperature, fire front intensity, fire speed) vary greatly from one burn to another (FORGEARD, 1987) but a distinction can be made between light or low intensity fires (soil-surface temperature <500°C) and high intensity fires (soil-surface temperature >500°C). On Brittany heathlands, spring fires are not always of low intensity. This should be set against findings by KAYLL (1966) and TRABAUD (1979) who indicated that summer fires were more intense than spring fires. Biocenotic response to fire, however, is also affected by season in which fire occurs.

How rapidly does habitat re-establishment occur after fire, and how does such re-establishment depend on fire intensity, season in which burning occurs, and the nature of pre-existing vegetation, respectively? Is species richness increased or decreased? Are herbaceous species favoured over ligneous species? These questions have been given particular attention in forest (AHLGREN, 1974; KOMAREK, 1974; LITTLE, 1974; PHILLIPS, 1974; WEAVER, 1974; RUNDEL, 1981) or Mediterranean ecosystems (BISWELL, 1974; NAVEH, 1974; DEBANO & CONRAD, 1978; TRABAUD, 1980). While heathland fires and their ecological consequences have been particularly well studied in Britain (WHITTAKER, 1961; KAYLL, 1966; GIMINGHAM, 1972; MALLIK & GIMINGHAM, 1983; HOBBS & GIMINGHAM, 1984) relatively little work has been undertaken in France (GEHU, 1960; GEHU & GEHU-FRANK, 1960; CLÉMENT & TOUFFET, 1981; GLOAGUEN & GAUTIER, 1981; METAILLIE, 1981).

This study examines and discusses features of vegetation regeneration on Brittany heathlands after experimental and natural burns.

METHODS

SAMPLE SITES

Sample sites were located on the west of the Paimpont upland area. Ground rock was Cambrian purple schist. Vegetation could be classed in one or other of two association types [*Ulici europaei - Ericetum cinereae* (LENORMAND, 1966; CLÉMENT *et al.*, 1978)] and [*Ulici minoris - Ericetum ciliaris* (LENORMAND, 1966; GEHU 1973)]. Soils were brown humus, brown acid, or brown hydromorphic. The main sample site features are shown in Table I. Controlled burn areas varied from 600 to 1,500 m^2. Natural burns could cover several hectares. Temperatures during controlled burns were measured both with thermo-sensitive varnishes and thermo-couples. Fire intensity was calculated using BYRAM's (1959) formula.

VEGETATION ANALYSIS

Vegetation re-establishment after fire was studied with line transects and permanent plots. Line transects (CANFIELD, 1941), provided a measure of relative species abundance. With sufficiently large numbers of contacts, and sufficiently small points contacts, measures of species frequency can be estimated using cover data (GREIG-SMITH, 1964; GODRON, 1968). Line transects measured between 20 and 50 m depending on apparent homogeneity in recolonizing vegetation. Measurements were made

TABLE I. — *Characteristics of the sites.*

SITE	Tall heathland					Low dry heathland			Mesic heathland	
Localization	Butte de Tiot	Trécesson	Chambre au loup	Coet-quidan	Coet-quidan	Coet f. ras	Coet f. moyen	Coet f. haut	Chambre au loup	Coet-quidan
Abbreviation	BT (LH)	Tr (LH)	CL (LH)	Coet (LHp)	Coet (LHe)	Coet (Lsr)r	Coet (Lsr)m	Coet (Lsr)h	CL (Im)	Coet (Lm)
Biomass (t/ha)	57,7	–	54,4	57,5	87,0	4,5	19,1	27,2	20,3	28,6
Soil	SBA	SBA	SBA	SBA	SBA	SBAhu	SBAhu	SBAhu	SBAHy	SBAHy
Line long (m)	30	50	20	20	20	20	20	20	20	20
FIRE										
No prescribed NP	NP	NP	C	C	C	C	C	C	C	C
Controled C										
Spring (P)	P+E	E	P	P	E	E	E	E	P	P
Summer (E)										
Intensity (kW/m)	–	–	6.800	3.800	2.700	400	1,200	1,600	3.000	600
Temperature (°C)										
maximal	–	–	570	930	580	480	530	530	470	760
at ground level	–	–	50	430	50	200	200	200	150	180
at − 1 cm	–	–	40	50-80	40	60-80	80-100	80-100	80	80

SBA = acid brown soil; hu = humiferous; Hy = hydromorphic; NP: natural burned site; C: experimental burned site.

every 10 cm with a 3 mm needle (200 to 500 readings per transect). Only species touching one side of the needle were recorded. Sampling interval was dependent on apparent rate of vegetation development.

Permanent plots (6.4 × 1.0 m) provided detailed vegetation maps, together with information on number and size of individual plants, or groups of plants, on cover, and dispersion. Maps for each species were made, adapting the point contact method as follows. Eleven 6.4 m line transects were spaced at 10 cm. Readings were made every 10 cm along each line (65 readings per line, 715 per plot).

Aboveground biomass was assessed from samples of all species and litter in ten 1 m × 1 m quadrats. Species were sorted, dried to constant weight at 65°C, and weighed. Litter was treated similarly.

STATISTICAL ANALYSIS

Fire at the Trécesson site was very violent, and subsequent vegetation re-establishment derived almost entirely from invading spores or seeds. The site is interesting both for this reason and because it had been studied before the fire. Detailed statistical analyses have been undertaken, and their mathematical basis has been discussed by TALLUR (1983; 1986) and TALLUR & FORGEARD (1988). They involve a new analytical approach, based on a hierarchical classification algorithm, with adjustment for contiguity. It is possible to isolate and characterize groups of successive points which are statistically homogeneous (patches). The analysis concerns data from a permanent 50 m line transect.

RESULTS

VEGETATION DEVELOPMENT IN DIFFERENT TYPES OF HEATHLANDS

Mesophilic heathland (*Coetquidan*)

Species re-establishment on a mesophilic heathland after a low intensity spring burn was very fast (fig. 1). Three weeks after burning, the hemicryptophytes (*Agrostis curtisii* and *Molinia coerulea*) had appeared, closely followed by the chamaephytes (*Erica ciliaris* and *Ulex minor*). One year later, cover attributable to the principal mesophilic heathland species was essentially derived from vegetation present before the burn.

Short dry heathland (*Coetquidan*)

Vegetation re-establishment by principal species after a low intensity summer fire was slow (fig. 2). Soil remained largely bare for nearly a year. *Agrostis curtisii* the most important species over this period, only covered 32% of the plot surface. Two and a half years later, total vegetation cover attained 90%, *Agrostis curtisii* cover was 65%, 2.5 times more abundant than before the burn. At the same date, *Ulex europaeus* and *Erica cinerea*, with 20.3 and 21.1% cover, respectively, were at only one third of their preburn coverage (70.0 and 67.9%). *Calluna vulgaris* re-established even more slowly, and was ten times less abundant (2.9%) after 3 years than before (29%).

Tall heathland (*Tiot*)

Vegetation development at a same site, subjected to fire at a seven year interval (summer fire 1976 and spring fire 1983) is illustrated in figure 3. After the summer fire, the dominant vegetation type from a structural point of view was composed of bryophytes for several months. An ephemeral stage dominated by *Funaria hygrometrica* preceded development of *Ceratodon purpureus*. However, *Polytrichum formosum* dominated other species from the start. *Agrostis curtisii* conferred a

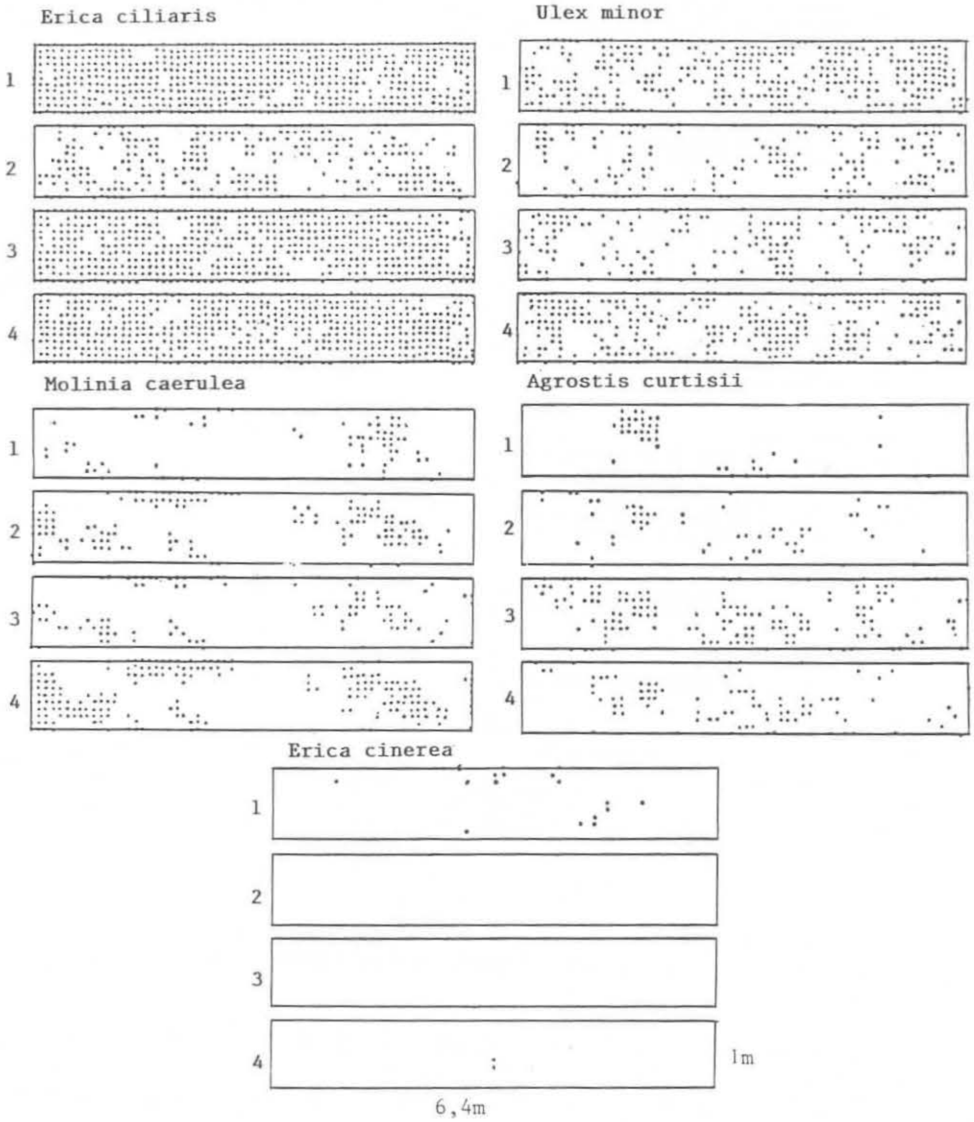


FIG. 1. — Evolution of the principal species of a mesic heathland after a fire [Coet (Lm) site]. 1, before fire; 2, 2 months after; 3, 7 months after; 4, 14 months after.

grassland aspect on the heath from the first to third years. Although present from the first year, Chaemaephytes only became dominant after the third. This was particularly so for *Ulex europeus* and *Erica cinerea; Calluna vulgaris* developed more slowly.

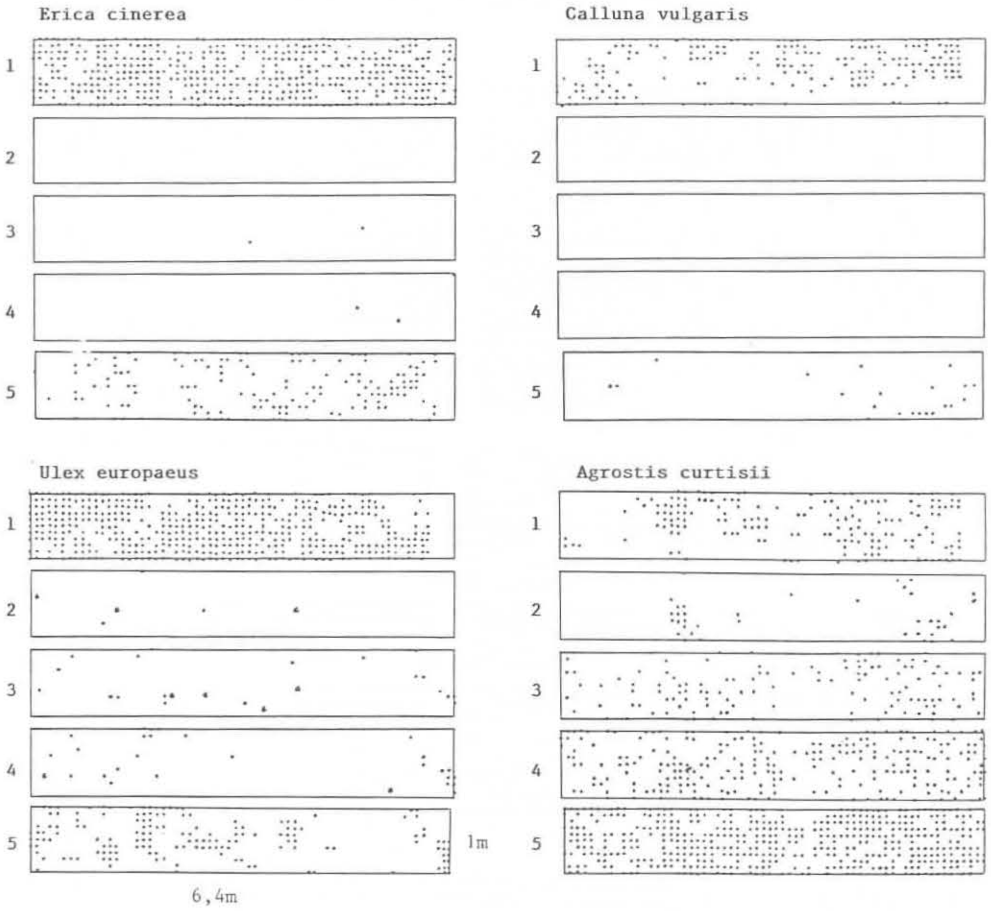
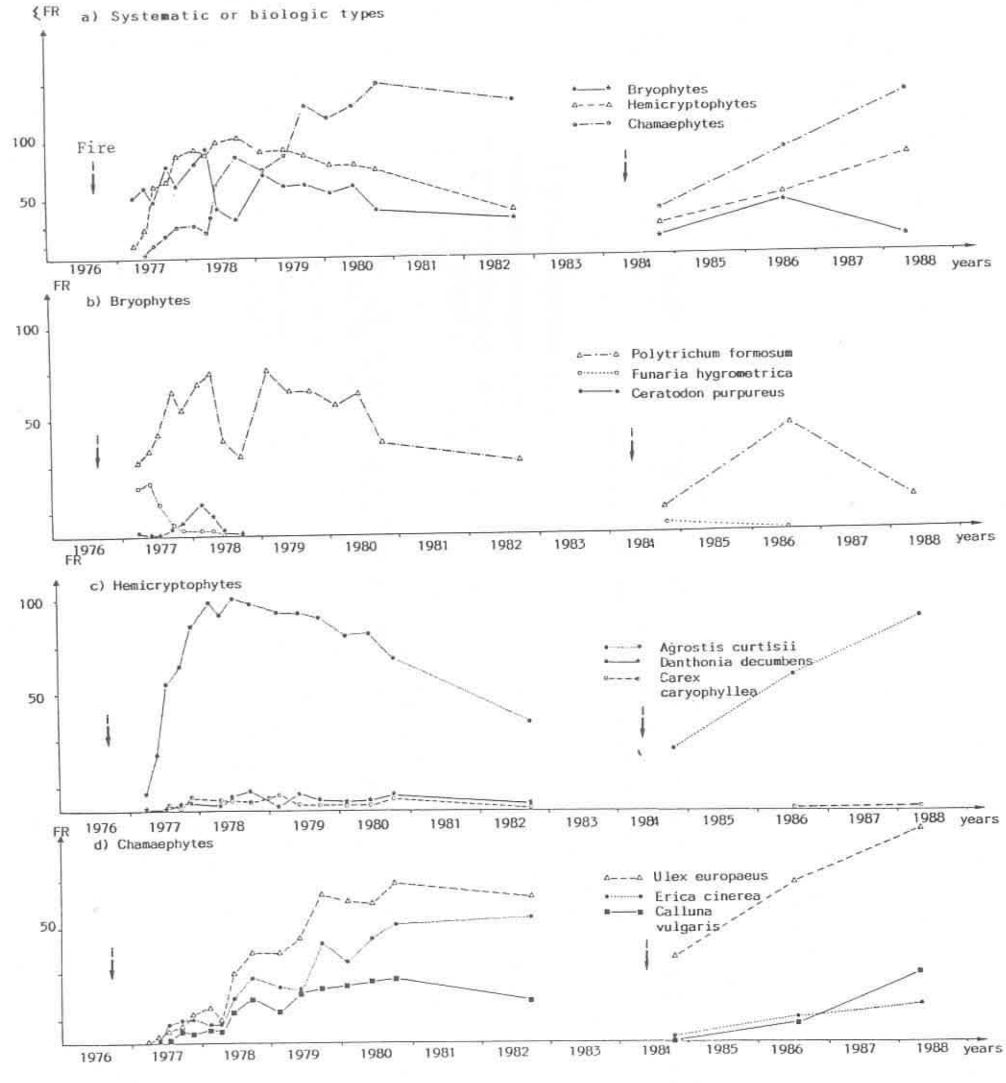


FIG. 2. — Evolution of the principal species of a dry low heathland after a fire [Coet (Lsr) site]. 1, before fire; 2, 2 months after; 3, 9 months after; 4, 14 months after; 5, 30 months after.

After the 1983 spring fire, vegetation development was much faster. Moss stages were absent or sparse, and development of *Agrostis curtisii* and heaths (*Erica cinerea* and *Calluna vulgaris*) less pronounced than before, whereas *Ulex europaeus* rapidly established tall cover (>90% at three years).

Tall heathland (Trécesson)

At the Trécesson site (fig. 4), which had experienced a violent summer burn, a moss layer, dominated by *Ceratodon purpureus*, developed to a maximum in the first year then decreased rapidly to disappear at the third year. The site was then still dominated by the bryophyte, *Polytrichum piliferum*. This attained maximal development in the second year after the burn, then decreasing progressively and disappearing in the ninth year. The bryophyte *Polytrichum formosum*, and the



FR relative species abundance

FIG. 3. – Evolution of the relative frequency of the biological or the systematic types and of the principal species of the tall heathland BT (LH). FR relative species abundance.

hemicryptophyte *Agrostis curtisii*, which had both been present from the start, became co-dominant from the fourth year. The aspect was then one of grass sward on a moss carpet up till the sixth year. *Polytrichum commune* then appeared, forming a bryophytic complex with *Polytrichum formosum*. After the sixth year, chaemaephytic species became dominant. *Erica cinerea* and *Ulex minor* developed

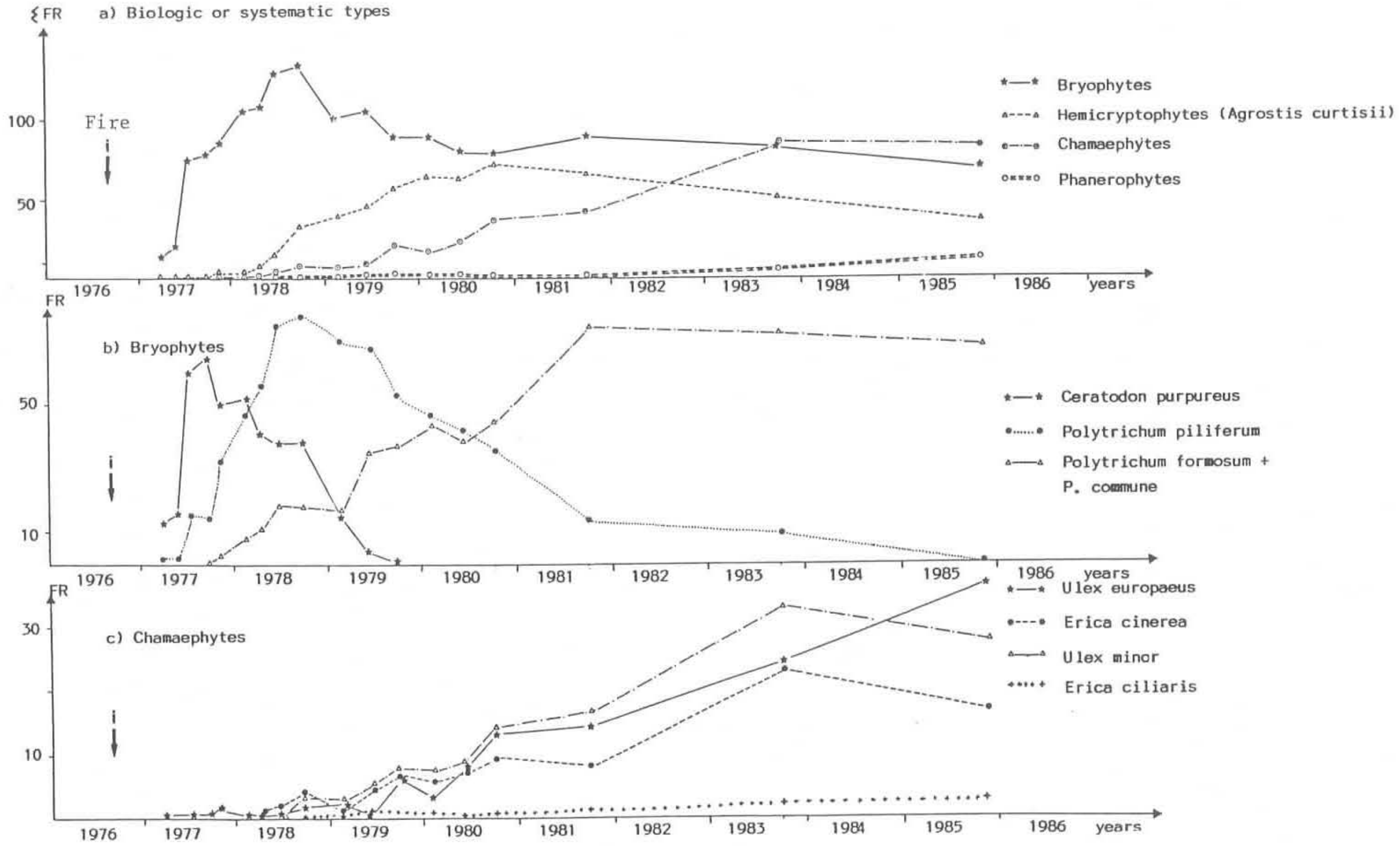


FIG. 4. — Evolution of the principal species of the tall heathland Tr(LH) after an intensive summer fire. FR relative species abundance.

similarly, their expansion apparently slowing down after the seventh year, whereas *Ulex europaeus* was still progressing.

If one considers the development of *Ulex europeus*, the principal species in this heathland type (fig. 5) fire intensity appears to have had more influence than season. Its cover had reached about 50% one year after a light spring fire (BT(LHp)), 2.5 years after a light summer fire (BT(LHe)), and 10 years after an intense summer fire (Tr(LH)).

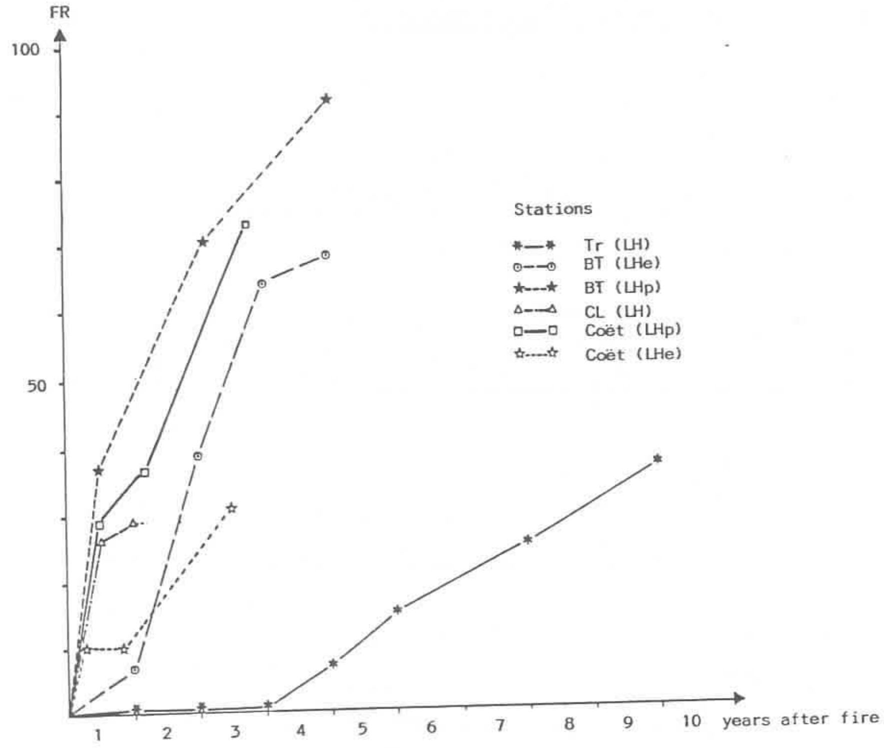


FIG. 5. — Evolution of the relative frequency of *Ulex europaeus* after different kinds of fire. FR relative species abundance.

DETAILED ANALYSIS OF A SITE SUBJECTED TO INTENSE BURNING (TRÉCESSON)

Statistical analysis revealed strong fragmentation (patchiness) in vegetation distribution along a 50 m line transect in the first years after burning, despite apparent homogeneity in bryophyte distribution (fig. 6). Ninety-two statistically homogeneous vegetation sequences or patches were initially detected. With time, vegetation became more uniform, and only 6 patches could be detected in 1985. The extent of these patches increased over time. One year after the burn, mean 'radius' of homogeneous patches was 0.54 m (+5.81%), it was 2.38 m (+7.94%) after 5 years, and had reached 8.33 m (+11.67%) at 9 years.

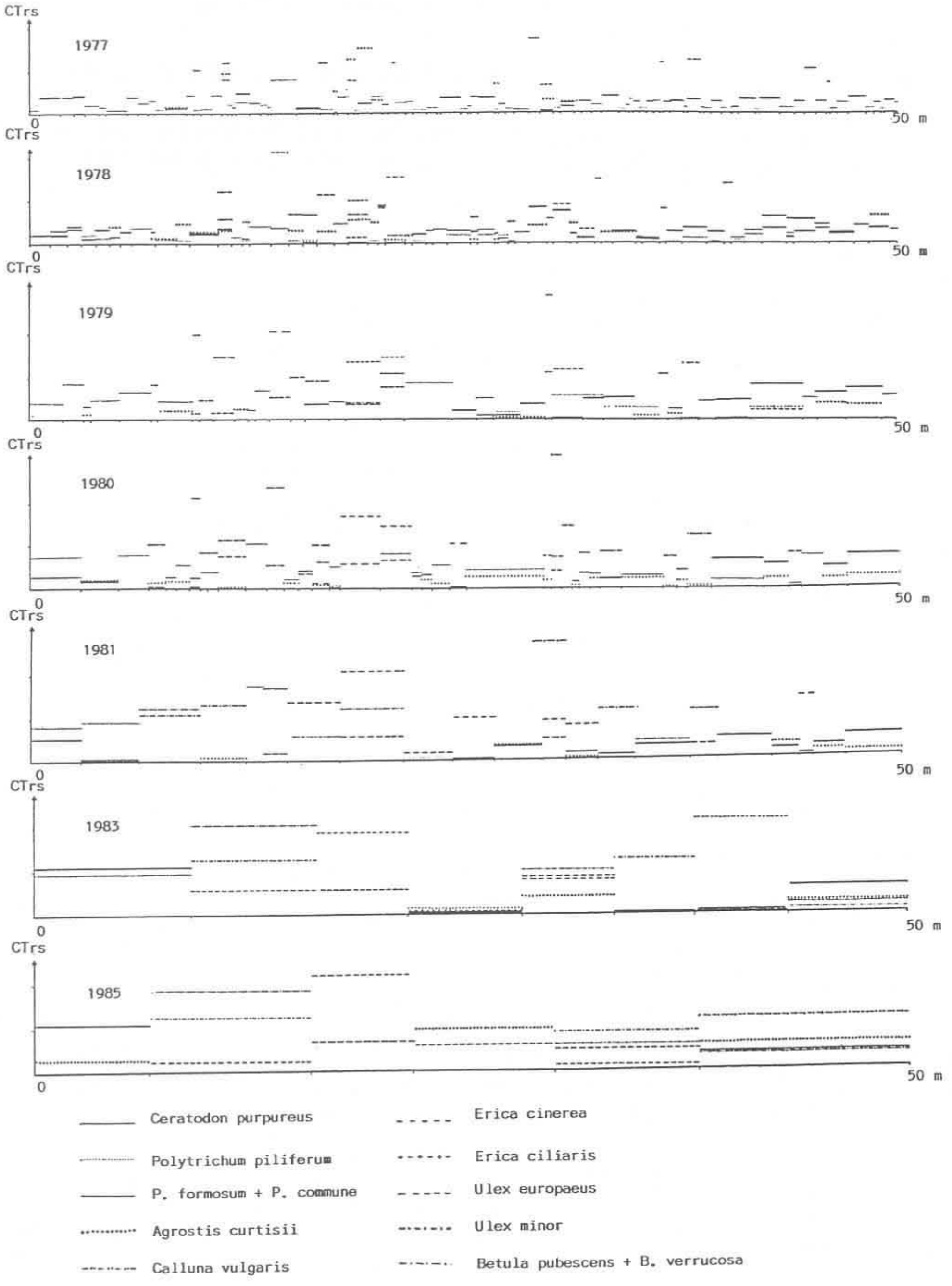


FIG. 6. – Evolution of the horizontal structure of a tall heathland subjected to an intensive summer fire (Tr(LH)), along a permanent line of 50 m. For each sequence, the species having the most important contribution (CTrs) and that characterize the sequence, are indicated.

This analysis and figure 6 clearly demonstrate two levels of competition, one within homogeneous patches, and one between neighbouring units. Inter-specific competition was reflected, for example, in progressive replacement of *P. piliferum* by *P. formosum* (or the bryophyte complex it forms with *P. commune*). Patches 1 and 2 on the line transect, between 1980 and 1985 exemplify this, with extension of the birch (*Betula*)-dominated patches at the expense of *Polytrichum*-dominated patches.

Global changes in species number and composition implied changes in number and composition of the different patches (92 initially identified along the line transect). Patch types were characterized by the dominant species. Changes are described and discussed here in terms of the percentage of any initial patch type, replaced by other given types (fig. 7). In other words, the percentage of initial type A replaced by type B, C, D... patches.

Forty-three percent of the original *Ceratodon purpureus* type patches were replaced (or eliminated) by *Polytrichum piliferum* patches, and 32% by *Polytrichum formosum* (or *P. formosum* + *P. commune*) type patches. Forty-three percent of *P. piliferum* patches were also replaced by *P. formosum* patches. *Polytrichum formosum* patches either developed towards mesophilic patches, with *Erica ciliaris* or *Ulex europeus* dominant, or remained as they were. *Erica cinerea* usually replaced *Agrostis curtisii*. In general *Erica cinerea* was gradually replaced by *Ulex europeus*. *Ulex minor*-dominated patches usually tended towards *Betula* type patches. Forty-six percent of *Ulex europaeus* patches, and 100% of *Betula* type patches persisted up to the end of the present study.

These measurements provide a general view of the pattern of vegetation re-establishment on the Trécesson plateau, over ten years following fire. Three main developmental trends emerge (fig. 8). The first of these is transition from *Ceratodon purpureus* to *Erica ciliaris*, passing through *Polytrichum* dominated bryophyte patches. The second is transition from *Ceratodon purpureus* to tall *Ulex europaeus* heathland, via an *Agrostis curtisii* sward and an *Erica cinerea*-dominated dry heathland. The third trend first takes one or other of the two paths already described, but then tends to a *Ulex minor* dominated mesophylic heathland type before transformation to *Betula* type pre-woodland.

Some of these vegetation structures may be intrinsically stable, and thus check any further development. This could be the case for *Polytrichum formosum* dominated patches, and *Ulex minor* heathland. Two more advanced developmental states, tall *Ulex europaeus* heathland, and birch scrub, could also be distinguished. The former is the end point under the driest conditions, and the latter for most mesic situations.

DEVELOPMENT OF VEGETATION BIOMASS AFTER FIRE

Biomass development was followed in tall heaths which had been subjected to spring (light) and summer (light and intense) burning (fig. 9 *a*). Measurements are expressed as percentage cover for each biological group (fig. 9 *b*).

Tall heathland (Tiot)

Biomass had been measured prior to the low intensity 1976 summer burn, as 55 t/ha (FORGEARD, 1977). At the time of the 1984 burn (*i.e.*, 7.5 years after the

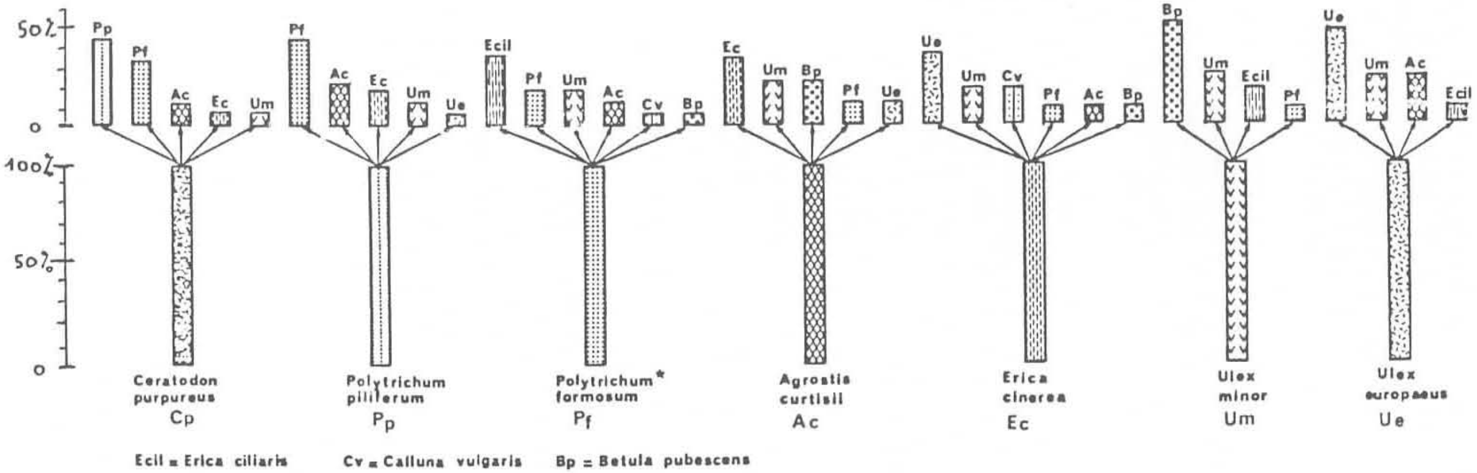


FIG. 7. – Gradual change of the sequences of vegetation between 1977 and 1985 at Tr(LH) site (in %).
(*) or bryophytic complex with *P. formosum* and *P. commune*.

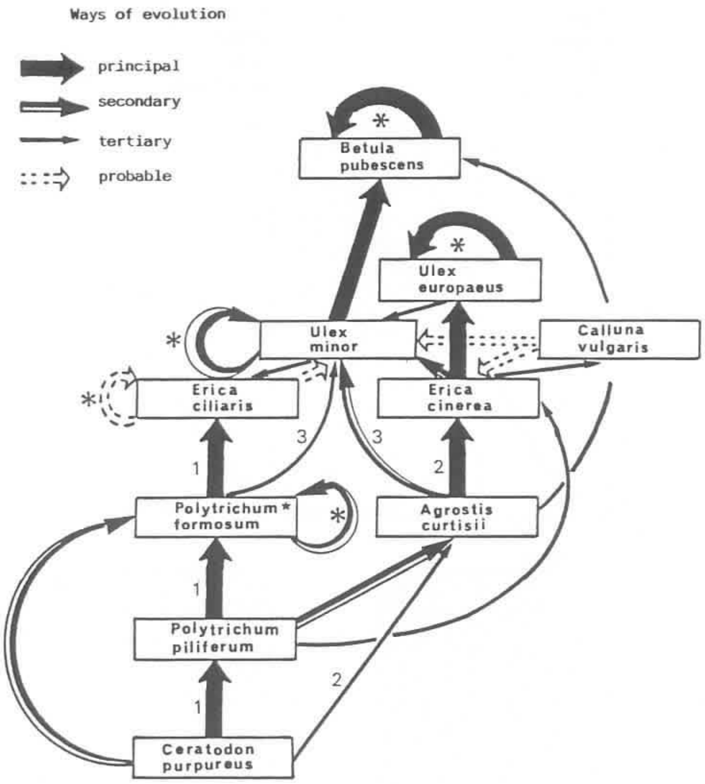


FIG. 8. — Evolution of the vegetation on the Trécesson site during the first 10 years following an intensive summer fire. (NB: in the rectangle appears the name of the principal species characterizing one of the sequences) (1-2-3 *see* the text).

first burn), that level had been re-established (fig. 9 *a* 2). This vegetation biomass, associated with a continuous horizontal vegetation structure, may be a critical threshold as regards fire-risk. During the first years immediatley following the spring fire, biomass re-establishment was three times faster than after the summer fire (fig. 9 *a* 2). If growth was to continue along the same pattern now, the Tiot heathland is likely to be at risk again in three to four years.

Tall heath at Trécesson

During the first years of vegetation re-establishment, phytomass was slightly greater than that measured after the summer fire at Tiot, but fell below this in the fourth year. The development of *Ulex europeus*, as indicated by permanent line transect, will result in strong phytomass increase in the years to come.

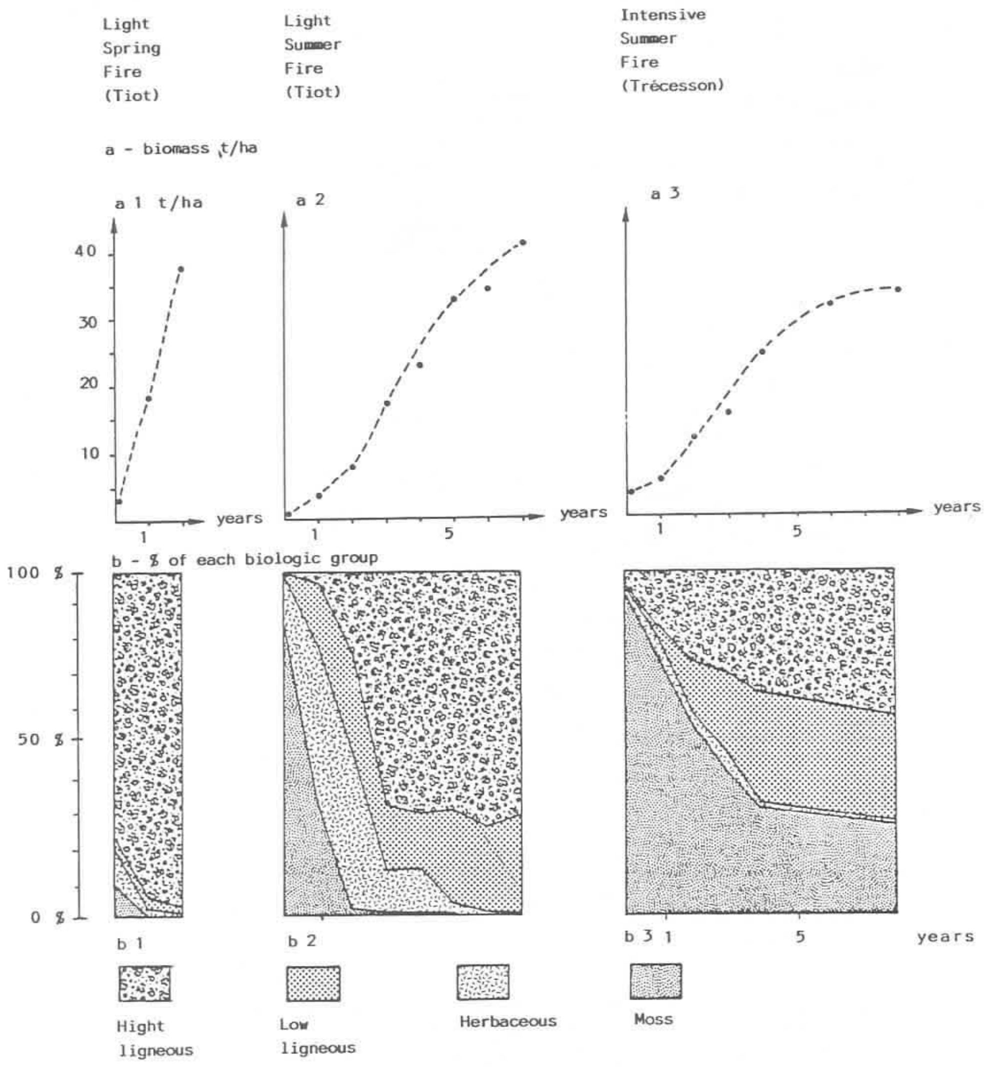


FIG. 9. — Evolution of the tall heathland biomass after different kinds of fire.

Species abundance in relation to fire type

The results discussed above are in general agreement with those obtained for relative species frequencies from permanent line transects. After a light spring burn (fig. 9 *b*1) biomass was composed essentially of the tall ligneous species like *Ulex europaeus*. After a light summer burn, (fig. 9 *b*2) mosses, herbaceous, low-woody and tall-woody species predominated in that order. After an intense summer fire (fig. 9 *b*3) mosses made a major contribution (as already indicated by measures of species frequencies). Net primary production of pioneer mosses reached 3.5 to

6.0 t/ha/yr (Forgeard, 1987) more than for some vascular plants in the region, 3 t/ha/yr for grass sward, 2 to 4 t/ha/yr for dry heathland, and 3 to 4 t/ha/yr for mesophyllic heathland (Forgeard, 1977). On the other hand, while *Agrostis curtisii* conferred a grassland aspect on the site for 2 years, and attained 70% cover, its biomass remained low.

DISCUSSION

Development of total cover

The appearance, development and disappearance of species or groups of species was related to the development of the vegetation as a whole and thus to total cover. Total cover is important, because after fire the soil surface is bare, and subjected to erosion. Rate of vegetation re-establishment itself affects extent to which soil erosion occurs. After a heath fire, the soil is rapidly covered by vegetation; in general, cover is complete by three years. Rate of vegetation re-establishment depended on several factors.

Fire intensity

Vegetation re-establishment was slower (table II) after a severe fire (at Trécesson) than after a light one (at Tiot). The intensity of these natural fires could not be determined, but the total disappearance of *Ulex europaeus* stems at Trécesson, while still present though burned at Tiot and Coetiquidan, can be taken to reflect both high fire intensity, and differences from one place to another.

Table II. — *Evolution of the vegetation cover and of the number of species.*

	COVER (%)				NUMBER OF SPECIES					
Site	=2 m	=6 m	=12 m	=36 m	Be . I	=2 m	=6 m	=12 m	=36 m	=108 m
BT (LH)	–	60	89	100	10	–	8	12	9	7
Tr (LH)	–	15	72	100	12	–	4	8	11	8
CL (LH)	15	35	68	–	4	1	4	10	–	–
Coet (LH) p	25	40	75	100	8	7	10	10	9	–
Coet (LH) e	10	25	66	100	5	0	1	11	12	–
Coet (Lsr) r	8	27	38	92	4	0	2	4	5	–
Coet (Lsr) m	6	21	37	91	5	0	2	3	6	–
Coet (Lsr) h	1	7	26	67	7	0	2	4	8	–
CL (Lm)	70	90	94	–	4	3	5	4	–	–
Coet (Lm)	65	70	95	–	6	4	6	6	–	–

Fire intensity alone is not, however, the only factor affecting vegetation re-establishment. At sites which had experienced similar fire intensities (3,000 to 4,000 kW/m) at sites Coet (LHe), Coet (LHp) CL (Lm) (table I), subsequent rate of vegetation cover varied considerably two months later (10, 25 and 70% respectively; table II).

Characteristics of pre-existing vegetation

Vegetation re-establishment on mesophyllic heaths after fire was rapid. Cover was 65 to 70% two months after fire (light at Coet-Lm, slightly more intense at

CL-Lm). Tall heaths recovered more slowly (10 to 25% at 2 months, 65%-75% after a year). Short dry heathland seemed to be far more sensitive, since cover was less than 10% at 2 months, and only attained 40% at 1 year.

Season

Season in which fire occurred had important consequences. Spring fires which occur before onset of vegetative growth had less affect on vegetation than fires in late summer. This is indicated by results from the Coetquidan tall heath (Coet LHe and Coet LHp). Two months after a spring fire, cover had reached 25%, whereas the figure was only 10% for a same interval after a summer fire. Nevertheless, 100% cover was established after three years in both cases.

DEVELOPMENT OF SPECIES NUMBER

Fire-caused changes in vegetation can be measured in terms of increase or decrease of species number. The sampling method was judged satisfactory since species number recorded for permanent line transects (200 to 500 sampling points, table II) did not differ from that for quadrats (715).

In tall heath, a slight increase in species number was usually observed for the three years immediately following the burn, but subsequently observed to decrease. On sites followed over ten years, the final total was lower than that prior to fire. In mesophyllic heaths, no such initial increase was observed.

Various indices have been used to determine degree of floristic stability in vegetation units. TRABAUD & LEPART (1980) proposed a 'fugacity index'. DIX (1960) used an index of similarity '*k*', equivalent in fact to that used by SORENSEN (1948). The following '*k*' values were found for the high heaths studied here. Trécesson 12; Tiot 32, Coetquidan, spring burn 55; summer burn 59. This demonstrates the higher degree of floristic modification after an intense summer burn. On the other hand, a low-intensity summer burn did not alter floristic composition more than a spring burn at Coetquidan. Mesophyllic heaths were not greatly disturbed by fire (Coet 80 to 90; CL 90).

These observations are comparable to those made by KRUGER (1983) in shrubland (chapparal, garrigue, heath, fynbos). An old vegetation stage had lower species number after fire than does a younger stage of the same type. Kruger noted that decrease in species richness was not necessarily progressive, starting from a peak immediately after the burn. Similar developmental patterns have been reported by other workers in Australia (SPECHT *et al.*, 1958; GILL, 1975; RUSSEL & PARSONS, 1978). Moreover, HOBBS *et al.* (1984) showed that in Calluna heathland, species number after burning was related to vegetation age at the burn. In heaths more than 15 years old, species number was much lower after fire, than for younger heaths.

In Brittany heathlands, fire results in initial short-term increase in species richness in tall heaths, but not in other types. There is an overall decrease in the long-term for all heathland types. The differences between tall heaths and others could be related to soil seed bank and its condition after fire, to the nature of external seed sources (anemo- and zoochory), to conditions for germination, or to seed predation.

GERMINATION AND STUMP REGENERATION IN RELATION TO RE-ESTABLISHMENT

The development of vegetation after fire depends on the nature of recolonization. When seeds are the principle source, development will often be slower than from stump regeneration. It is also evident that the subsequent vegetation structure will be more similar to the original when stump regeneration has been the main source, rather than seeds.

Re-colonization on study sites was mainly from seeds on tall heath at Trécesson and on short dry heath at Coetquidan. On the other tall heaths it was mainly from germination and stump re-growth. On mesophyllic heath the main source was stump re-growth.

Germination

Heath species establish large dormant soil seeds banks (GRIME, 1979; RIVIÈRE, 1979). Fire can have two contrasting effects, either destroying seeds, or stimulating germination. Lethal temperatures are around 200°C, but between 40 and 120°C germination rate is increased (GIMINGHAM, 1972). *Calluna vulgaris* and *Erica cinerea* seeds have better germination rates when submitted to 80°C for 2 minutes (GOMA-TCHIMBAKALA, 1981; BAHUON, 1982). Although temperature conditions during heath fires (table I) would therefore seem likely to generally favour germination, there was no appreciable germination of heath species. It may be that, although germination was stimulated, microclimatic conditions (notably humidity) were unfavorable, or that competitive factors were operative.

Stump regrowth

Calluna vulgaris stump regeneration has been well studied in Britain. It depends on plant age, fire temperature, and season. When soil surface temperatures reach 500°C for more than a minute, plants die whatever the age (WHITTAKER, 1960). Regeneration is better for stands aged between 6 and 10 years, and becomes difficult for those 15 years or older (GIMINGHAM, 1960, 1972; MILLER & MILES, 1970).

On study sites discussed on this paper, heathland age (10 years) and fire temperatures allowed stump regeneration. Vigorous growth recorded on mesophyllic heath could have been related to soil conditions, notably humidity. Under these conditions *Erica ciliaris* and *Ulex minor* would have been in competition. Table III shows that gorse invaded space more rapidly than heather. Since fire conditions

TABLE III. — *Development of* Erica ciliaris *and* Ulex minor *on 3 plots on Coet (Lm) site. Density of presence on 715 observation points; % in bold type.*

Species	P1		P2		P3	
Erica ciliaris						
before	595	**83,2**	639	**89,4**	670	**93,7**
+ 14 m.	613	**85,7**	588	**82,2**	503	**70,3**
result	+ 18	**+ 2,5**	− 51	**− 7,1**	− 167	**− 23,5**
Ulex minor						
before	180	**25,2**	359	**50,2**	370	**51,7**
+ 14 m.	221	**30,9**	319	**44,6**	442	**61,8**
result	+ 41	**+ 5,7**	− 10	**− 5,6**	+ 72	**+ 10,1**

were favourable both to germination and stump regeneration, between-site differences in speed and type of recolonization could be due to mesophyllic conditions, inter-specific competition, or allelopathic phenomena.

THE RELATIVE IMPORTANCE OF HERBACEOUS AND LIGNEOUS SPECIES

Fire has been commonly used to favour development of herbaceous vegetation for grazing (GIMINGHAM, 1972; METAILLIE, 1981; KRUGER, 1984). Vegetation type before burning, and its developmental pattern after burning can be examined using a triangular diagram (fig. 10) of the same kind as is used to represent soil texture. Short dry heath (Coet Lsr) was class **L** before fire, and class **H** one year afterwards. Herbaceous was clearly favoured over ligneous vegetation. Tall heaths (Coet LHp, CL LH) were classed **L** before fire, sites BT LH, Coet LHe were classed L (h), and site Tr LH (Trécesson) was classed **L** (m). Although fires there favoured herbaceous species, vegetation was tending to woody structure after three years. In one intense summer fire at Tr LH, this development was virtually direct from bryophyte to woody species, herbaceous species being relatively inconspicuous at all times. Mesophyllic heaths were L (h) type before fire. Herbaceous species were slightly favoured in the first year (H (l)) after burning, but from the second year on, no difference was apparent between pre- and post-burn composition. In conclusion,

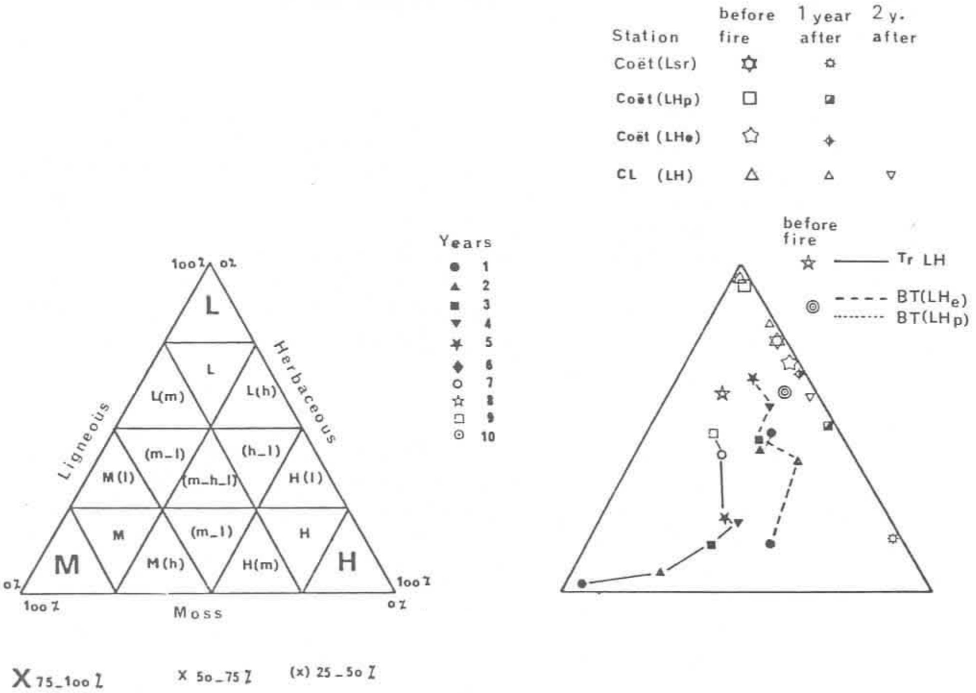


FIG. 10. — Triangle of floral composition. Determination and evolution of the floral class of the heathlands after fire.

fire gives a slight temporary advantage to herbaceous species in Brittany heathlands. This effect is more evident in tall heaths and dry heaths.

BIOMASS TREND AND CRITICAL THRESHOLD

Measures of vegetation biomass after fire showed that the quantity established in tall heath implied high fire risk seven years after a spring fire, and 10 to 15 years after a summer fire. In Brittany it was not possible to study a sufficiently wide heath age-range, which could have allowed identification of post-fire developmental phases of the kind considered by BARCLAY-ESTRUP & GIMINGHAM (1969) and BARCLAY-ESTRUP (1970). These authors distinguished four developmental stages in *Calluna* heaths. The first, a pioneer phase up to 6-10 years, with low biomass, maximal production, and vascular plants other than *C. vulgaris* dominant. The second from 7-15 years, one of construction with high *C. vulgaris* biomass and maximal production, those of other species being minimal. The third phase, 15-25 years, is the mature phase, biomass is maximal, production falls, *C. vulgaris* is on the decrease, and other species on the increase. The fourth phase, 20-33 years, is one of degeneration, with biomass still high, but productivity minimal.

CLÉMENT & TOUFFET (1976) distinguished 3 stages in the Monts d'Arrée heathlands of Brittany. A first stage of early development, lasting about four years, with graminaceae dominant and maximal net production. A second stage extended up to the eighth year with falling production and woody plants dominant. Finally a third stage of re-structuration, with rapidly increasing productivity, and nanophanerophytes becoming more abundant. In contrast, it is difficult to detect a comparable developmental model for the Paimpont heathlands studied here, given the variety in developmental pattern after burning.

CONCLUSION

Re-establishment of plant cover described in this paper corresponds with what MILES (1982) described as a fluctuating model, for the heathlands subjected to light fire (vegetation changes while retaining the same general features), and to a secondary successional model for heathlands subjected to intense fire.

First successional stages in strongly disturbed heathland are characterized by their bryophyte component. It may be that increase in pH, from ash ionic contribution, favours rapid development of *C. purpureus*, a well known colonizer of burnt ground (RICHARDSON, 1981). The species began to develop at Trécesson in March 1977, *i.e.*, 8 months after the fire. It is likely that colonization was due to spores produced in December and in early spring, carried into the denuded zone, favourable to their establishment. With decline in soil ion-content, *Polytrichum* species can establish (FROMENT, 1975; SOUTHORN, 1976). No measurement of bryophyte soil spore bank was attempted, but, as for *C. purpureus*, an external source seems more likely than extension of a moss carpet derived from spores present in soil before the burn. These species are known to have high spore production, and the spores can be carried over large distances (ZANTEN, 1978).

For higher plants the soil stock of viable seeds was low after intense fire at Trécesson (RIVIÈRE, 1979). *Agrostis curtisii* germinated and developed rapidly after fire, an observation which accords with SWEENEY (1956). Initial seed arrival may be attributed to wind and animal transport. Few viable woody plant seeds remained after the fire, but since fire intensity varied, germination of some survivors may have been stimulated. Re-establishment of heaths and gorse could have been appreciably favoured by animal transport, but no specific information was obtained on this point.

The developmental phases after major disturbance, discussed in detail above, involve resumption of growth by surviving plants or seeds, immigration, seedling establishment and inter-specific competition.

When species which develop after fire, are those present before, vegetation changes reflect growth rate, reproductive potential, and differential survival of species concerned (see also DELARZE & WERNER, 1985). Models advanced by CONNELL & SLATYER (1977) are applicable to events at Trécesson. These are the facilitation model, in which species can only become established after habitat changes due to others, the tolerance model in which species establish themselves, irrespective of pioneer action, and the inhibition model, in which pioneer species prevent or delay establishment of others.

Under less intense disturbance, stump regeneration is predominant (as in the mesophyllic heathlands of the present study). Re-colonization then results in re-establishment of 'initial floristic composition' and is essentially derived from a pre-existing floral reserve (EGLER, 1954).

Choice of an appropriate vegetation recolonization model for given conditions (fluctuation or secondary succession) will depend essentially on fire intensity. Rate of vegetation re-establishment depends on the nature of the vegetation before fire, and season in which fire occurs. Thus it is faster after spring fire in mesophyllic heathland and slower after a summer fire in short-dry or tall heathland.

Heathlands are species poor systems, subject to relatively little change in floral composition due to fire. Fire only favours herbaceous species in the short term, and not in terms of biomass, even if such species confer a grassland aspect for some time.

The observations made in the present study, and considerations raised above, emphasize the problem of both spatial and temporal study scale.

After fire, heathland floral composition is usually comparable to that prior to the fire after ten years. Fire in Brittany heathlands is recurrent, and disturbance at short or long-term is dependent on its intensity. However, fire also maintains and perpetuates heathland formation by preventing transition to woodland climax. Nevertheless, more severe fire may open the way to this end point by opening up habitat for a sufficiently long time. This does not happen after light fire because woody shrubs regenerate quickly and prevent tree seedling establishment. Thus, as CLEMENT (1987) commented "Heathland emerges as a robust dynamic vegetation formation, and heathland species are active pyrophytes. Recurrent cutting and burning may well, perhaps, have had an appreciable selective action on the plant species characteristic of heathland".

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